2216

DYNAMICS OF THE DEAD WOOD CARBON POOL IN NORTHWESTERN RUSSIAN BOREAL FORESTS

O. N. KRANKINA and M. E. HARMON

Department of Forest Science, Oregon State University, Corvallis, Oregon 97331, USA

Abstract. Our study examines dead wood dynamics in a series of permanent plots established in closed, productive second-growth forest stands of north-west Russia and in temporary plots that represent different successional stages and types of disturbance. Dead wood stores measured on 63 plots 0.2–1.0 ha in size range from 1–8 Mg C ha^{-1} in young to mature intensively managed stands, 17 Mg C ha^{-1} in an old-growth forest, 20 Mg C ha^{-1} on a clear-cut, and 21–39 Mg C ha^{-1} following a severe windthrow. A total of 122 logs, snags, and stumps aged by long-term plot records was sampled for decay rates and to develop a system of decay classes. Annual decomposition rates are: 3.3% for pine, 3.4% for spruce, and 4.5% for birch. Based on these decay rates the average residence time of carbon (C) in the dead wood pool is 22–30 years. The mortality input on the permanent plots was 23–60 Mg C ha^{-1} over 60 years of observation or 15–50% of the total biomass increment. This data suggests a dead wood mass of 10–22 Mg C ha^{-1} would be expected in these mature forests if salvage had not occurred. In old-growth forests, dead wood comprised about 20% of the total wood mass, a proportion quite similar to the larger, more productive forests of the Pacific Northwest (USA). If this proportioning is characteristic of cool conifer forests it would be useful to estimate potential dead wood mass for old-growth forests without dead wood inventories. However, the use of a single live/dead wood ratio across the range of successional stages, a common practice in C budget calculations, may substantially over- or under-estimate the dead wood C pool depending upon the type of disturbance regime. Intensive forest management including short harvest rotations, thinning and wood salvage reduces dead wood C stores to 5–40% of the potential level found in undisturbed old-growth forest. In contrast, natural disturbance increases dead wood C pool by a factor of 2–4.

Keywords. DEAD WOOD, CARBON CYCLE, RUSSIAN FORESTS, DECAY RATES, BIOMASS POOLS.

1. Introduction

One of the most important questions facing ecologists today is the role of the biota in the global carbon (C) cycle. The fact that 20–50% or 1–3 Pg yr^{-1} of the annual fossil fuel C can not be accounted for (Post *et al.*, 1990; Dixon *et al.*, 1994) raises serious questions about our current understanding of this cycle. Moreover, the recent decrease in atmospheric concentrations can not be fully explained; oceanic uptake cannot account for it (Sarmiento, 1993). Recent efforts to decrease uncertainty of global C cycling processes have focused upon improved estimates of land-use change in the tropics (Dale *et al.*, 1991), sequestration in soil humus (Schlesinger, 1990), increased production associated with CO_2 fertilisation (Keeling *et al.*, 1989), and sequestration by temperate forests (Tans *et al.*, 1990). Despite years of study it has recently become clear that we still do not understand the current role of forests in controlling the global C cycle (Dixon *et al.*, 1994). Over the past few years forests have been described as everything from a source (Houghton *et al.*, 1987) to a sink of C (Tans *et al.*, 1990).

We suggest there may be another fundamental problem with current global C budgets: dead trees and associated woody detritus are generally not considered (Kobak, 1988; Houghton and Woodwell 1989; Post *et al.*, 1990). At best this pool is included as a constant proportion to live biomass (Kolchugina and Vinson, 1993). There are many reasons why, until recently, there has been little research on this topic (Harmon *et al.*,

Water, Air and Soil Pollution **82**: 227–238, 1995.

1986). First, decomposition of woody detritus is a long-term process and, as with other long-term ecological processes (i.e., forest succession), there are few long-term observational studies (Franklin *et al.*, 1990). Second, inappropriate methodology has been used to study dead wood dynamics. For example, litter production is often estimated from a sample area <10 m^2 for 1–2 years, and although this is suitable for fine litter, it is inappropriate for woody detritus which requires many hectare-years for reliable estimates (Sollins, 1982). Finally, there are few estimates of dead tree stores because they have little commercial value and until recently were associated with "unhealthy" forest or bad management practices. Thus little empirical data exists upon which to base estimates or ground assumptions.

Ignoring dead trees has several profound impacts upon our understanding of global C dynamics. First, it excludes a flux at least as large as fossil fuel burning. Recent global estimates of tree mortality indicate 3–15 Pg C yr^{-1} of woody detritus is produced within intact stands, while natural catastrophic disturbances add another 1 to 2 Pg yr^{-1} globally (Harmon *et al.*, 1993). Second, the size of the terrestrial detrital pool has been underestimated by 85–295 Pg C (Harmon and Chen, 1991; Harmon *et al.*, 1993). If woody detritus was in steady-state this might not be a major concern, but land-use changes have placed woody detritus in disequilibrium. In the Pacific Northwest, for example, reduction of woody detritus accounted for 33% of the C flux to the atmosphere associated with the conversion of old-growth forests to plantations (Harmon *et al.*, 1990). If this is a general rule, then past calculations of C flux from forest clearing have been underestimated. It also implies that a large, unaccounted for C sink may be present in forests recovering from past harvest (Harmon and Chen, 1991). Third, excluding dead trees will lead to an unrealistic assessment of the response of detrital stores to projected climate change. Analysis of transient responses to projected climate change indicate a large pulse of C may be injected into the atmosphere as forests are disturbed or migrate (King and Neilson, 1992). To a large degree, the temporal dynamics of this transient pulse will be controlled by the decomposition of woody plants killed by catastrophic disturbances (i.e., fire), or increased stress. Fourth, estimated effect of intensive forest management on C sequestration (Sedjo and Solomon, 1991; Dixon *et al.*, 1991) would probably be reconsidered if woody detritus could be taken into account. The commonly held notion that young forests are active C sinks does not hold if the flux from decomposing dead wood is included in calculations (Cohen *et al.*, in review). We have found that in managed forests, when woody detritus removed by timber harvest, salvage operations, and firewood gathering is included total ecosystem C stores can be substantially decreased (Krankina and Harmon, 1994).

Clearly the time has come to begin including woody detritus in the global C cycle. However, with the currently available database it is extremely difficult to advance beyond order of magnitude estimates. To date the majority of work concerning the production, decomposition, and storage of C in dead trees has centred in the Pacific Northwest. Now the United States National Science Foundation and Earthwatch funding has allowed us to study the woody detritus production via tree mortality, as well as the dead wood decomposition and stores in the taiga forests of north-western Russia. Russian forests comprise about 50% of the globe's boreal forests and thus play a significant role in the global C cycle (Kobak, 1988). Russian taiga forests have a great potential in explaining the missing C sink yet our understanding of these forests is inadequate and their overall impact remains uncertain: some authorities consider it a major sink and others a source of CO_2 (Kolchugina and Vinson, 1993; Melillo *et al.*, 1988).

The goal of this paper is to examine the dynamics of woody detritus in relation to tree species, successional stage, management and disturbance regime in a Russian boreal forest based on preliminary results of our on-going research. To the best of our knowledge this is the first time that empirical data on long-term decomposition rates for Russia's major boreal tree species has been published.

2. Study Area and Methods

The study area is located at about 59°N and between 31°E and 32°E in the St. Petersburg and Novgorod Regions of north-western Russia. The climate is cool maritime with cool wet summers and long cold winters. The area is a part of the East-European Plain with elevations between 0 and 250 m above sea level; terrain is gentle and rests on ancient sea sediments covered by a layer of moraine deposits. Soils are mostly of podzol type on deep loamy or sandy sediments. Natural vegetation of the area belongs to southern taiga types; major dominant conifer species include Scots pine (*Pinus sylvestris* L.) and Norway spruce (*Picea abies* (L.) Karst.) both growing in pure and mixed stands. After disturbance, they are often replaced by hardwoods including birch (*Betula pendula* Roth.) and aspen (*Populus tremula* L.).

Experimental data for this study was collected in closed forest stands of medium to high productivity subject to intensive forest management. Although this data set does not represent the average for the region, it allows us to examine woody biomass distribution and the impact of management practices on C stores at stand level in intensively managed forest types.

Our work takes advantage of a permanent plot system started over 60 years ago to study effects of thinning upon forest growth in St. Petersburg (then Leningrad) region in north-western Russia. Most plots were set up in 1928–34 and supplemented by new plots in 1968–76 at the Leningrad (now St. Petersburg) Forestry Research Center (Sennov, 1984). The plots were set up in well stocked young stands (23–45 years old) and over their existence they were regularly remeasured at 4–11 year intervals so that by now an age span of 20 to 105 years is covered by the record. Each site consists of a control plot and 1 to 4 thinned plots with 15–50% of the growing stock removed. The size of each plot is 0.1–0.25 ha. The historical data on live tree measurements currently maintained by St. Petersburg Forest Academy is supplemented by one plot established in an old-growth spruce stand and 8 plots (including 3 controls) in a windthrow area by the St. Petersburg Forest Academy and by 4 temporary plots set up by the authors on recent clear-cuts. The scope of work includes: (1) estimation of decay rates; (2) live and dead wood inventory; (3) reconstruction of dead wood dynamics over succession.

A chronosequence approach was used to estimate decomposition dynamics of the three major species: birch, pine, and spruce. The time elapsed since the tree died was estimated based on plot records. A chronosequence is a substitution of space for time. Although not as precise as time series measures, chronosequences can give a valid first approximation of temporal dynamics. Two major problems associated with most chronosequences are avoided in this study. The first problem is uncertainty of the time of death, a minor problem in our case as the time of death will be known within ±3 years from the plot records. In the case of thinned trees, the exact year of death could be determined. The second problem involves lack of information concerning initial conditions of dead trees. This is an especially large problem when fragmentation has occurred; major underestimates of decay losses and nutrient flux can be made if fragmentation losses are ignored (Harmon and Chen, 1991). Fragmentation is not a major problem in our case because the diameter at the time of death was recorded, thus the original volume and mass can be accurately estimated. Each of the three species to be examined had a chronosequence sampled in the plots of at least three sites. Each chronosequence consists of 2–12 trees in each of 5 age/decay classes (Figure 1). The total of 122 logs, snags, and stumps was sampled to estimate average density for decay classes. Out of these, 75 were dated and used to develop the chronosequences.

For each log, snag or stump sampled, we recorded length, diameters, and bark cover, and noted external characteristics associated with the degree of decomposition. Cross-sections were then removed using a chainsaw to measure the density of the bark and wood. To account for the variation within logs, three to four cross-sections were taken systematically along the length of the bole. The maximum and minimum diameter and height above the root collar of each cross-section was recorded. For each cross-section the density and radial thickness of the bark, sapwood, and heartwood as well as the depth and type of decay (white rot *versus* brown rot) was measured. In the case of extremely decayed cross-sections, the external dimensions were recorded prior to removal to estimate sample volume. Mass was determined after oven drying at 55 °C until constant weight was reached. Sample density was calculated as dry mass divided by green volume.

To calculate the average density of each sampled log or snag we weighed sample densities by respective section volumes. Density values were then averaged by decay classes for each tree species. The result of this work was the decay class system that allows to convert the dead wood volume into biomass (Table I). To account for mass loss through fragmentation for dated logs and snags, residual density was calculated by dividing current biomass by the estimated bole volume at the time the tree died (Harmon *et al.*, 1987). Average decomposition rate of dead wood was estimated using regression of the residual density over time:

$$\text{density}_t = \text{density}_0\,[\exp(-kt)] \qquad [1]$$

where t is the time elapsed since the tree died, density_t is the residual density, density_0 is the initial density, and k is the decomposition rate.

Live and dead aboveground tree biomass was measured in the 63 plots. Live tree biomass was calculated by standard procedures based on diameter and height measurements of trees in each plot and on local forest mensuration tables (Tretyakov *et al.*, 1952; Moshkalev *et al.*, 1984). A biomass to C conversion factor 0.5 was used. As dead wood is commonly overlooked in biomass assessments and C budget calculations we describe the methods for this component in greater detail.

Measurements of dead wood stores in the plots followed the methods procedures described in Harmon *et al.* (1986, 1987). Within each plot the end diameters and lengths of each piece of dead wood >10 cm diameter and >1 m in length was recorded. All forms of coarse dead wood were inventoried including snags (standing dead), logs (dead and downed), stumps (cut by harvest), and "blobs" of highly decayed wood. We did not inventory wood buried in the forest floor, although this can be a substantial proportion of that layer (Little and Ohman, 1988). Species and decay state of each piece were also noted. The mass was calculated by multiplying computed volume by the average bulk density of each decay class and species. Total organic mass was converted to C stores by assuming the C content of dead wood was 51% (Sollins *et al.*, 1987). Live tree and dead wood C stores were compared for old-growth and early successional forest including clear-cut, young (10–20 years after harvest), middle aged (30–70 years after harvest), and mature second growth forest (80–120 years after harvest). Where possible the effect of natural disturbance (windthrow), thinning and salvage was assessed. Successional stages beyond the limits of observations on permanent plots were reconstructed using local growth and yield tables (Tretyakov *et al.*, 1952; Moshkalev *et al.*, 1984) and live/dead wood ratios from the measured temporary plots (Figure 2).

Mortality input into the dead wood pool over time was calculated for several selected plots over the 60-year observation period based on the long-term records of the St. Petersburg Forest Academy (Sennov, unpublished data) and using the same biomass equations as for live trees (Tretyakov *et al.*, 1952; Moshkalev *et al.*, 1984). Decomposition rates applied to mortality inputs allowed us to reconstruct the dynamics of dead wood stores on the control and on the thinned plots (Figure 3). Comparison of reconstructed and measured dead wood stores provided an estimate of the impact of salvage.

TABLE I

Decay class system for Russian boreal tree species.

Species	Decay class	Density ± STD (Mg C m^{-3})	Sample size (dated samples)	Mean age (yr)*
Pine	1	0.201 ±0.018	10 (6)	3
	2	0.160 ±0.037	14 (10)	8
	3	0.117 ±0.032	17 (12)	16
	4	0.071 ±0.042	12 (7)	29
	5	0.065 ±0.002	3 (2)	70
Spruce	1	0.169 ±0.030	6 (6)	4
	2	0.159 ±0.028	15 (11)	7
	3	0.106 ±0.029	10 (5)	12
	4	0.038 ±0.005	3 (0)	-
Birch	1	0.251 ±0.017	5 (5)	1
	2	0.236 ±0.038	5 (2)	4
	3	0.142 ±0.035	13 (5)	14
	4	0.063 ±0.036	9 (4)	20

*Based on 75 dated logs.

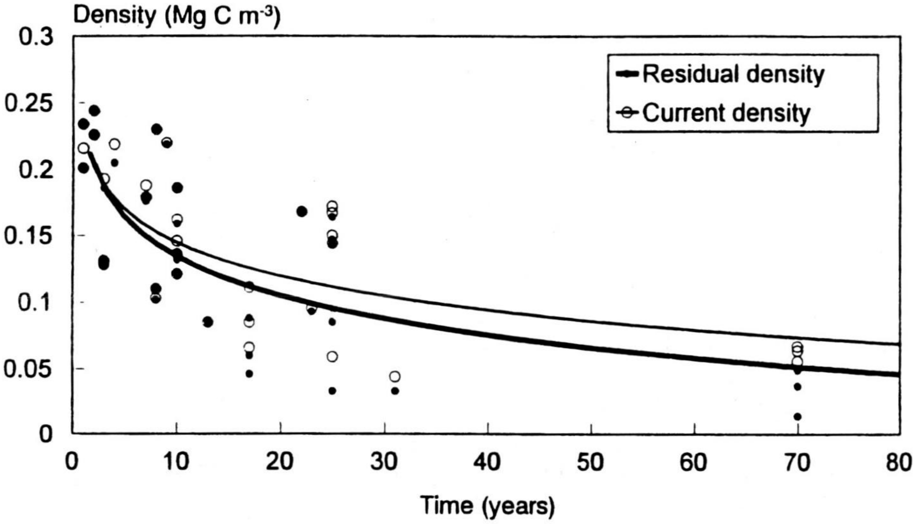

Fig. 1. Chronosequence of dead wood density for pine. Due to fragmentation current density is higher than residual density (current biomass of a dead tree divided by its initial volume).

3. Results

The decay class system relates the 5 decay classes for each of the 3 studied species to density values (Table I). The changes in density values with decay classes depend on initial density which is considerably higher for birch than for conifers and on the dynamics of decomposition process. Spruce and birch logs at final stages of decay were not found in studied plots resulting in missing density values in class 5. This may be due to the fact that these two species were decayed by white rot fungi, a functional group that does not leave lignin, the materials typically found in the decay class 5 boles (McFee and Stone, 1966).

The loss of density over time does not fully account for the loss of biomass by a dead tree because it does not include the loss of volume due to fragmentation. In the advanced stages of decay density values change little because fragmentation removes the most decayed material (Figure 1).

Average annual decay rates (±90% confidence interval) for pine, spruce and birch are 3.3 ±0.6%, 3.4 ±1.0%, and 4.5 ±1.3% respectively. Due to a significant variation in decay rates of individual logs, the correlation between the residual density and the time elapsed since the tree died is rather low, with r^2 ranging from 0.67 to 0.81. These decay rates generally agree with the common assumptions that birch decomposes faster than conifers, and that pine retains higher density in the advanced stages of decay because of the slow decomposition of its heartwood. Based on these decay rates the average residence time of C in the dead wood pool is 22–30 years depending on species.

In these forests, the position of a dead tree (log *versus* snag) is an important control at the early stages of decomposition. For example, the average density of pine snags during the first 10 years is equal to the sound wood density (0.205 Mg C m^{-3}) indicating

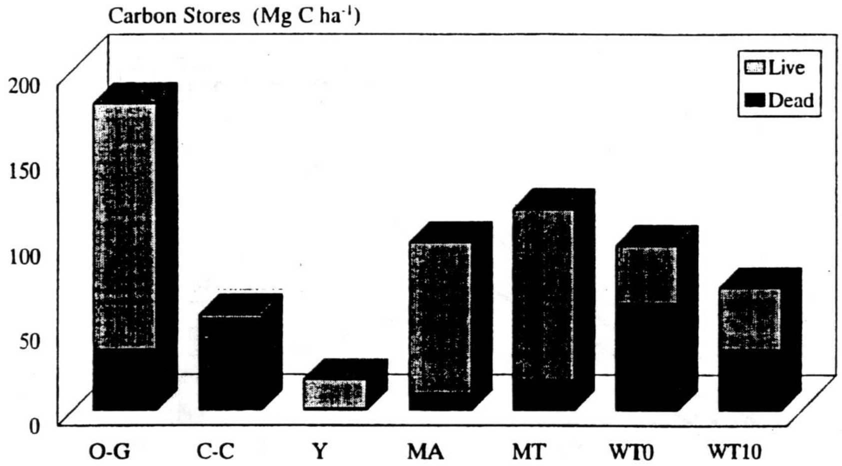

Fig. 2. Successional dynamics of live biomass and dead wood on a productive site (reconstruction based on local growth tables and live/dead wood ratio from measured plots): O-G: old-growth, C-C: clear-cut, Y: young, MA: middle age, MT: mature, WTO: following windthrow, WT10: 10 years after windthrow.

little decomposition occurred during this period. In contrast, the density of pine logs on the ground of the same time period is 0.145 Mg C m^{-3}, which represents a 27% biomass loss (the difference is significant at 0.0013 level). Similarly, spruce and birch logs lost more biomass compared to snags by 25% and 39%, respectively. As snags rarely appear to stand longer than 10 years, this decrease in decay rates is a temporary phenomenon.

Dead wood stores vary significantly over succession and do not necessarily parallel the dynamics of live biomass (Figure 2). The largest amount of dead wood was found in recently disturbed areas. Nearly all above-ground biomass present on a clearcut was in dead wood store which measured 20 Mg C ha^{-1}. Another site that was recovering for 10 years after a severe windstorm had 21–39 Mg C ha^{-1} in dead wood or 43–57% of the total biomass found on the site. Dead wood stores immediately following this windstorm, estimated by applying undecayed densities to class 2 and 3 log volumes, are even higher (39–52 Mg C ha^{-1} or 59–69% of total biomass). Dead wood stores are minimal in young stands (10–40 years old) regenerating after clearcut harvest and in older second-growth stands where dead wood is salvaged (1–8 Mg C ha^{-1}). In undisturbed old-growth forest, woody detrital stores measured 17 Mg C ha^{-1} or 20% of the total aboveground biomass.

The dynamics of woody detritus on permanent plots were reconstructed using the data on dead wood input by tree mortality adjusted for losses to decomposition (Figure 3). The mortality input on the control plots was 23–60 Mg C ha^{-1} over 60 years of observation or 15–50% of the total above-ground biomass increment. Thinning reduced tree mortality: on thinned plots it was 4–26 Mg C ha^{-1} or 7–12% of the total biomass increment. Our reconstruction of dead wood dynamics indicates significant accumulation of woody detritus with stand age. Predicted dead wood stores (10–22 Mg C ha^{-1}) were higher than those actually measured in the plots due to salvage operations.

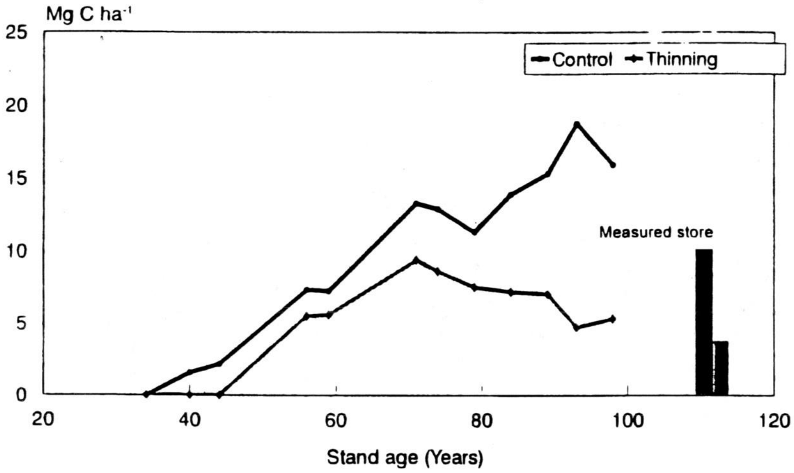

Fig. 3. Reconstructed dead wood dynamics in a pine stand over the period of observations and measured dead wood store at the end of the period (example).

4. Discussion

Comparison to other carbon pools

This study indicates a considerable pool of woody detritus can be found in boreal forests. The estimated range for undisturbed forests of 17–36 Mg C ha^{-1} is similar to the stores found in surface litter (10–32 Mg C ha^{-1}) measured on the same plots, but is less than the mass of organic matter stored in the very shallow but highly organic soil (57–128 Mg C ha^{-1}) (Sennov, 1984; Kobak, 1988). In forests disturbed by fire, which consumes much of the litter and organic soil, or by clearcut harvest, which removes much of the live biomass, woody detritus can become the dominant store of organic matter and C within the ecosystem, making 98% of above-ground biomass on a clearcut and 59–69% following a windthrow.

Our estimates of woody detritus for boreal forest ecosystems may be low for two reasons. First, we did not consider the wood associated with dead coarse roots and branches. This could increase our estimates up to 30% depending upon the degree of sprouting in top killed trees, the difference between above- and below-ground decay rates, and the effect of size on decay rates. Second, we did not consider wood buried within the soil and forest floor in our inventories. Including these other forms of woody detritus would increase our estimates of total woody detritus in these forests.

Comparison to other biomes

The mass of dead wood depends upon a number of factors including the productivity of the ecosystem, climate, substrate quality, and organisms degrading the material (Harmon *et al.*, 1986). As latitude increases the production rate of dead wood should decrease along with the overall productivity of the forest (Harmon *et al.*, in press). Although this should lead to lower dead wood stores, this trend is partially offset by a decrease in the decomposition rate caused by a decrease in temperature and macro-invertebrate abundance (e.g., termites), and by more frequent disturbances. Comparison of our study results to other major biomes indicates that dead wood C pool in undisturbed Russian boreal forest is generally within the range of that reported for some other forest regions: 9–21 Mg C ha^{-1} in undisturbed dry tropical forests (Harmon *et al.*, in press), 2–25 Mg C ha^{-1} in moister tropical forests (Kauffman *et al.*, 1988; Edwards and Grubb, 1977; Uhl and Kauffman 1990), 15–25 Mg C ha^{-1} in cold deciduous forests (Gore and Patterson, 1986; Harmon *et al.*, 1986; Tritton, 1980) or pine dominated conifer forests where 14–21 Mg C ha^{-1} of coarse woody debris has been reported (Fahey, 1983; Harmon *et al.*, 1986). In contrast, woody detrital stores in boreal forests are much smaller than those found in cool, moist conifer forests which range between 100 and 225 Mg C ha^{-1} (Agee and Huff, 1987; Grier and Logan 1977; Spies *et al.*, 1988), but exceed those reported for warm temperate deciduous forests where 10–12 Mg C ha^{-1} is typical (Muller and Liu, 1991; Onega and Eickmeir, 1991; Harmon *et al.*, 1986; Harmon and Chen, 1991). This comparison suggests there is no simple correlation between woody detrital mass and latitude.

Decomposition rates

The rates of decomposition that we estimated for the dominant conifer species in north-western Russia (0.033–0.034 yr^{-1}) are generally higher than for other northern ecosystems. Red spruce and balsam fir in the north-east USA decompose at rates of 0.0299 yr^{-1} (Lambert *et al.*, 1980) to 0.029–0.033 yr^{-1} (Foster and Lang, 1982). In western Canada lodgepole pine and Engelmann spruce had a wide range of decay rates (0.0025–0.0299 yr^{-1}) depending upon the age of forest (Johnson and Greene, 1991). Lodgepole pine had a rate of 0.027 yr^{-1} reported for central Oregon (Busse, 1994) and a lower rate of 0.016 yr^{-1} in a cool dry Wyoming site (Fahey, 1983). As these species are similar to those we studied, we would conclude that the overall environment in north-western Russia is slightly more favourable to wood decomposition than many other northern forests.

Decomposition rates of birch were lower than the 0.11 yr^{-1} reported for warmer hardwood dominated forests (Onega and Eickmeier, 1991). Although there been no reported studies on birch, another hardwood species, aspen, is reported to decompose at a rate of 0.05 yr^{-1} in Minnesota (Miller, 1983). Our observations indicate the aspen decomposes faster than birch in Russian forests, so we can not judge the degree to which climate is affecting hardwood decomposition rates.

Influence of disturbance and succession

Disturbance plays a major role in determining the amount and nature of the dead wood. The most obvious effect of disturbances is to increase the amount of woody detritus. In the forests we studied, clear-cutting and windthrow increased woody detrital levels 1.5–1.7 and 2.5–3.8 fold, respectively. This increase is similar to a fire killed *Pseudotsuga/Tsuga* forest in which woody detritus increased 2.7 fold (Agee and Huff, 1987) and a logged tropical forest which had woody detritus increase 3.4 fold (Uhl and Kauffman, 1990; Harmon *et al.*, in press).

Russian boreal forests are frequently disturbed and should contain a significant pool of disturbance related dead wood. Forest fires occur annually on about 3 million hectares of forest land in Russia (Dixon and Krankina, 1993); windthrow is also fairly widespread: in 1990 it was reported on 30 000 ha but the actual extent could be even greater (Krankina *et al.*, in press). Predicted climate change is expected to increase disturbance frequency and severity, which may result in a significant positive feedback to greenhouse gas accumulation in the atmosphere (King and Neilson, 1992). Understanding the dynamics of dead wood is critical for assessing the scope and timing of this feedback.

As the time since a disturbance increases, the mass of dead wood in disturbed forests should decrease dramatically. Given the decomposition rates observed here, we would expect the disturbance generated wood to largely disappear within 65–90 years depending upon the species composition of the disturbed forest. For that reason dead wood stores reach minimum in young stands. The average density of dead wood in a young stand (0.07–0.10 Mg C m^{-3}) is about one half that in an old-growth forest because harvest generated residues have lost most of their biomass while there is no measurable mortality input from the new generation of trees. The density values are the highest (0.15–0.18 Mg C m^{-3}) following disturbance that generates a pulse of tree mortality.

The post-disturbance recovery of dead wood stores to old-growth levels depends upon the decay rate and time required to restore input or mortality to old-growth rates (Harmon *et al.*, 1986; Harmon and Chen, 1991). The recovery of the woody detritus pool is delayed by thinning and dead wood salvage for firewood (Figure 3), which are widely practised in populated areas of Russia. While increasing biomass output and economic efficiency, which is the goal of traditional forestry, these intensive forest management practices significantly reduce C stores in forest ecosystems (Krankina and Harmon, 1994; Lamas and Fries, 1994).

Since experimental data on dead wood C stores and flux is very rare it is important to develop methods of estimation based on other more readily available parameters, such as live biomass. Our measurements show that in Russian old-growth forests, dead wood comprised about 20% of the total wood mass, a proportion quite similar to the larger, more productive forests of the Pacific Northwest (USA) (Krankina and Harmon, 1994). If this proportioning is characteristic of cool conifer forests it would be useful to estimate potential dead wood mass for old-growth forests without dead wood inventories. However, we also found tremendous variation in dead wood stores largely controlled by disturbance and management practices (Figure 2). On our plots the share of dead woody in total above-ground biomass stores ranged from 2 to 98%. The use of a single live/dead wood ratio across the range of successional stages, which is a common practice in C budget calculations, may substantially over- or under-estimate the dead wood C pool depending upon the type of disturbance regime.

Dynamics of dead wood can also be estimated if mortality input and decomposition rates are known. There is a substantial body of information regarding tree mortality associated with disturbance (e.g., Auclair, 1985) and values of tree mortality for undisturbed stands can be found in many growth-and-yield tables. However, the process of decomposition needs to be studied further to develop adequate modelling tools to dynamically estimate C pools and flux associated with woody detritus.

Acknowledgments

The research was sponsored by the National Science Foundation (BSR-9213187) and in part by Earthwatch Center for Field Research. The authors gratefully acknowledge helpful assistance of Drs. S. N. Sennov, A. V. Gryazkin, E. S. Melnikov, and A. V. Selikhovkin of St. Petersburg Forest Academy (Russia) who provided access and background information on their research plots and Dr. O. G. Chertov for facilitating co-operation between Russian and United States participants of the project. We also thank the Oregon State University Forest Science Data Bank (FSDB) and Gody Spycher, for assistance in managing and processing the data used in this paper.

References

Agee, J. K. and Huff, M. H.: 1987, *Can. J. For. Res.* **17**, 697-704.

Auclair, A. N. D.: 1985, *Can. J. For. Res.* **15**, 279-291.

Birdsey, R. A.: 1992, *Gen. Tech. Rep. WO*-59, 51 pp.

Busse, M. D.: 1994, *Soil Sci. Soc. Am. J.* **58**, 221-227.

Cohen, W. B., Wallin, D. O., Harmon, M. E. and Fiorella, M.: (Unpublished manuscript).

Dale, V. H., Houghton, R. H. and Hall, C. A. S.: 1991. *Can. J. For. Res.* **21**, 87-90.

Dixon, R. K. and Krankina, O. N.: 1993, *Can. J. For. Res.* **23**, 700-705.

Dixon, R. K., Schroeder, P. E. and Winjum, J. K.: 1991, EPA report 600/3-91/067.

Dixon, R. K., Brown, S., Houghton, R. A., Solomon, A. M., Trexler, M. C. and Wisniewski J.: 1994, *Science* **263**, 185-190.

Edwards, P. J. and Grubb, P. J.: 1977, *J. Ecol.* **65**, 943-969.

Fahey, T. J.:1983, *Ecol. Monogr.* **53**, 51-72.

Foster, J. R. and Lang, G. E.: 1982, *Can. J. For. Res.* **12**, 617-626.

Franklin, J. F., Bledsoe, C. S. and Callahan, J. T.: 1990, *Bioscience* **40**, 509-523.

Franklin, J. F., Shugart, H. H. and Harmon, M. E.; 1987, *Bioscience* **37**, 550-556.

Gore, J. A. and Patterson, W. A. III: 1986, *Can. J. For. Res.* **16**, 335-339.

Grier, C. C. and Logan, R. S.: 1977, *Ecol. Monogr.* **47**, 373-400.

Harmon, M. E. and Chen, H.: 1991, *Bioscience* **41**, 604-610.

Harmon, M. E., Franklin, J. F., Swanson, F. J., Sollins, P., Gregory, S. V., Lattin, J. D., Anderson, N. H., Cline, S. P., Aumen, N. G., Sedell, J. R., Lienkaemper, G. W., Cromack, K. Jr. and Cummins, K.: 1986, *Adv. Ecol. Res.* **15**, 133-302.

Harmon, M. E., Cromack, K. Jr. and Smith, B. G.: 1987. *Can. J. For. Res.* **17**, 1265-1272.

Harmon, M. E., Ferrell, W. K. and Franklin, J. F.: 1990, *Science* **247**, 699-702.

Harmon, M. E., Brown, S. and Gower, S. T.: 1993, *In:* Vinson, T. S. and Kolchugina, T. P. (eds.) *Carbon Cycling in Boreal and Sub-Arctic Ecosystems*, EPA Number 600-93/084, Corvallis, USA, pp. 167-178.

Harmon, M. E., Whigham, D. F. and Sexton, J.: *Biotropica*, (In press).

Houghton, R. A. and Woodwell G. M.: 1989, *Sci. Amer.* **260**, 36-44.

Houghton, R. A., Boone, R. D., Fruci, J. R.,. Hobbie, J. E, Melillo, J. M., Palm, C. A., Peterson, B. J., Shaver, G. R., Woodwell, G. M., Moore, B., and Skole, D. L.: 1987, *Tellus* B **39**, 122-139.

Johnson, E. A. and Greene, D. F.: 1991, *J. Veg. Sci.* **2**, 523-530.

Kauffman, J. B., Uhl, C. and Cummings, D. L: 1988, *Oikos* **53**, 167-175.

Keeling, C. D., Bacastow, R. B., Carter, A. F., Piper, S. C., Whorf, T. P., Heimann, M., Mook, W. G. and Roeloffzen, H. J.: 1989, *Geophysical Monogr.* **55**, 165-236.

King, G. and Neilson, R. P.: 1992, *Water, Air, and Soil Pollution* **64**, 365-383.

Kobak, K. I: 1988, *Biotical Compounds of Carbon Cycle.* Gidrometeoizdat Publishers, Leningrad, Russia.

Kolchugina, T. P. and Vinson, T. S.: 1993, *Water, Air, and Soil Pollution* **70**, 207-221.

Krankina O. N. and Harmon, M. E.: 1994, *World Resour. Rev.* **6**(2), 161-177.

Krankina, O. N., Dixon, R. K., Shvidenko, A. Z. and Selikhovkin, A. V.: *World Resour. Rev.*

Lämås, T. and Fries, C.: 1995, *In: Forest Survey Designs: 'Simplicity versus Efficiency' and the assessment of Non-timber Resources,* Proceedings of Conference, 2-7 May, 1994, Monte Verità, Switzerland, Swiss Federal Institute of Technology, Swiss Federal Institute of Forest, Snow and Landscape Research, and IUFRO S4.02/S4.11. (In press.)

Little, S. N. and Ohmann, J. L.: 1988, *Forest Science* **34**, 152-164.

Lambert, R. C., Lang, G. E. and Rieners, W. A.: 1980, *Ecology* **61**, 1460-1473.

McFee, W. W. and Stone, E. L.: 1966, *Soil Sci. Soc. Am. Proc.* **30**, 513-516.

Melillo, J. M., Fruci, J. R. and Houghton, H. A.: 1988, *Tellus* B **40**, 116-128.

Miller, W. E.:1983, *Forest Science* **29**, 351-356.

Muller, R. N. and Liu, Y.: 1991, *Can. J. For. Res.* **21**, 1567-1572.

Onega, T. L. and Eickmeier, W. G.:1991 *Bull. Torrey Bot. Club* **118**, 52-57.

Post, W. M., Peng, T. H., Emanuel, W. R., King, A. W., Dale, V. H., and DeAngelis, D. L.: 1990, *American Scientist* **78**, 310-326.

Sarmiento, J. L: 1993, *Nature* **365**, 697-698.

Schlesinger, W. H.: 1990, *Nature* **348**, 232-234.

Sedjo, R. A. and Solomon, A. M.: 1991, *In: Greenhouse Warming: Abatement and Adaptation. Proceedings for the Workshop, Washington, USA.* pp. 105-19.

Sennov, S. N.: 1984, *Tending the Forest: Ecological Basis.* Lesnaya Promyshlennost, Moscow, Russia, [In Russian]

Sollins, P.:1982, *Can. J. For. Res.* **12**, 18-28 1982

Sollins, P., Cline, S. P., Verhoven, T., Sachs, D. and Spycher, G.: 1987, *Can. J. For. Res.* **171** 1585-1595.

Spies, T. A., Franklin, J. F. and Thomas, T. B.: 1988, *Ecology* **69**, 1689-1702.

Tans, P. P., Fung, I. Y., and Takahashi, T.: 1990, *Science* **247**, 1431-1438.

Tretyakov, N. V., Gorskiy, P. V., and Samoilovich, G. G.: 1952, *Forest Inventory Reference Book.* Goslesbumizdat Publishers, Moscow-Leningrad, Russia. [In Russian]

Tritton, L. M.:1980, Ph.D. Dissertation, Yale Univ., New Haven, USA.

Uhl, C. and Kauffman, J. B.: 1990, *Ecology* **71**(2), 437-449.